Analysis of productivity of radiata pine plantations under different silvicultural regimes using the 3-PG process-based model

Rolando Rodríguez[1], Miguel Espinosa[2], Pedro Real[2] and Juan Inzunza[3]

[1]Corporación Nacional Forestal, Barros Arana 215, 2º piso, Concepción, Chile
Email: rorodrig@udec.cl
[2]Departamento de Silvicultura, Facultad de Ciencias Forestales, Universidad de Concepción, Casilla 160-C, Concepción, Chile
[3]Departamento de Física, Facultad de Ciencias Físicas y Matemáticas, Universidad de Concepción,
Casilla 160-C, Concepción, Chile

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Summary

The effects of crown structure and management of site resources on production of wood were studied. Growth and development of three stands with agroforestry management were compared with a traditionally managed stand. The 3-PG model, validated through stem analysis, was used to estimate growth. It was concluded that the leaf area index was strongly controlled by the plantation design and final stand density. The fertilisation regime had positive effects on leaf area index but its potential was limited by crown structure. In the traditional forestry regime, increment of stem wood biomass was strongly related to leaf area index. In stands with agroforestry management, however, stem increment was associated with changes in allocation of carbohydrate from the biomass of fine roots, caused by fertilisation. Final production of wood is more affected by thinning, because of the effect of thinning on crown structure, than by the availability of site resources. The maximisation of wood production will depend upon the combined management of site resources and the intensity and opportunity of thinning.

Keywords: productivity; simulation; site occupancy; 3-PG model; radiata pine; *Pinus radiata*

Introduction

Wood production in forest plantations depends upon the rate of canopy photosynthesis and the proportion of photosynthate allocated to stem growth (McMurtrie *et al.* 1990). Canopy photosynthesis depends on leaf area and carbon assimilation rate per unit leaf area or leaf mass (Wang and Jarvis 1990). Hence, carbon gain is determined by the availability of site resources such as light, water and nutrients (Carlyle 1995). However, there is an inverse relationship between carbon assimilation rate per unit area and leaf area index. Tree size, crown structure and stand density also influence carbon gain and carbon partitioning (Perry 1985; Roberts *et al.* 1993), so wood production rates are likely to be influenced by stand structure as well as site resources and environmental factors (Waring and Running 1998). Perry (1985) and Cannel (1989) stated that crown size and structure have more influence than site resources on wood production. McMurtrie and Landsberg (1992) showed, for radiata pine (*Pinus radiata* D. Don), that the availability of resources such as water and nutrients is more important than stand structure for the production of photosynthate and its allocation to stem.

Process-based models have been developed for the analysis of the processes that affect carbon gain and carbon allocation to the different tree components. These models have great potential utility as research tools for silviculture and can become valuable instruments supporting decision-making processes for sustainable forestry (Mäkelä *et al.* 2000a). Process-based models describe the effects of the physical environment on physiological processes (Landsberg and Hingston 1996; Waring and Running 1998) and the interdependence of water, carbon and nutrient cycles (Running and Gower 1991; McMurtrie and Landsberg 1992; Waring and Ryan 1995).

One of the most widely used process-based models is the 3-PG model developed by Landsberg and Waring (1997) (Fig. 1). It is being tested in natural and plantation forest in the United States (Landsberg *et al.* 2000; Coops and Waring 2001), in South Africa (Dye 2001), in New Zealand (White *et al.* 2000) and Australia (Coops *et al.* 1998; Sands and Landsberg 2001).

In this study the 3-PG model was used to analyse the productivity of radiata pine stands growing under different silvicultural regimes. We examined the hypothesis that plantation design and final density, determined by the thinning regime that affects the potential leaf area index, are more important factors than site resources for explaining wood production.

Materials and methods

Study area and experimental design

A silvopastoral agroforestry experiment was established by the Corporación Nacional Forestal, in Tanumé, community of Pichilemu, VI Region, Chile (34º09'–34º15'S; 72º53'–72º59'W). Soils in this area are classified as Alfisols, suborder Xeralfs. The region has a sub-humid temperate climate, with four to six months of drought annually. The study site has an annual average precipitation of 703 mm, with a minimum average temperature of 8.6ºC and a maximum average temperature of 15.4ºC. Data

Table 1. Management regimes, initial densities, layout and types of pasture for the experimental treatments of radiata pine

Management regime	Initial (and final)[a] density (trees ha^{-1})	Plantation design	Pasture type	Symbol
Silvopastoral	625 (187)	Cluster	Sown	T1
Silvopastoral	625 (181)	Cluster	Natural improved	T2
Silvopastoral	1000 (185)	Bands	Sown	T3
Forestry	1600 (489)	Normal	Natural	T4

[a] The numbers in parentheses indicate actual density at 16 y of age

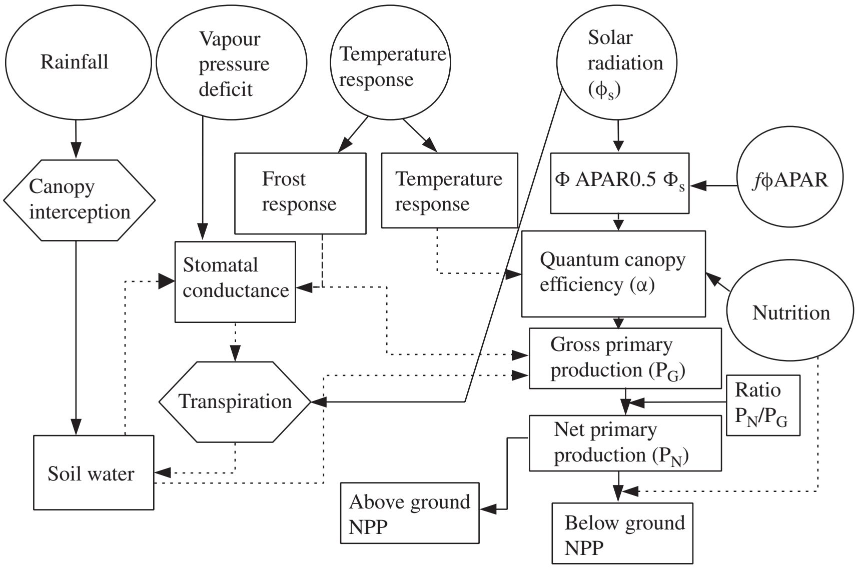


Figure 1. Schematic of the simplified 3-PG model to predict forest growth (N. Coops, *pers. comm.*)

were obtained from the meteorological station at Tanumé, located 2.5 km from the study site, during the years 1983 to 1999.

The experiment, established in the winter of 1983, consisted of radiata pine planted at two initial densities: 625 and 1000 trees ha^{-1} in units of 6 ha. Two years later, pasture was established in combination with the plantations and they became modules of a silvopastoral system. There were two types of pasture: naturally improved, fertilised every 4 y; and sown and fertilised annually. The 625 trees ha^{-1} consisted of an arrangement of four plants in clusters at a spacing of 2 m × 2 m, with 6 m × 6 m between clusters. The 1000 trees ha^{-1} consisted of an arrangement in bands, with distances between trees of 2 m × 3 m and between bands of 7 m. In a contiguous area a plantation was established with an initial density of 1600 trees ha^{-1} spaced at 2.5 m × 2.5 m (Table 1) for the sole purpose of wood production. The silvicultural treatment in all of the stands consisted of thinning in 1989, 1991 and 1993 and pruning in 1988, 1990 and 1993. The timing, intensity and residual density were oriented towards optimisation of the silvicultural system and identification of the best combination for tree and pasture growth.

3-PG model

The 3-PG model is described by Landsberg and Waring (1997) (see also Sands and Landsberg 2001). It has the following structure:

i) The model calculates total carbon fixed or Gross Primary Production (P_G) from utilisable, absorbed photosynthetically active radiation (φ_{pau}) and a canopy quantum efficiency (α_C). The value for φ_{pau} is obtained by a reduction of the value of the utilised photosynthetically active radiation (φ_{pau}) by modifiers — coefficients whose values vary between 0 and 1. The modifiers reflect the constraints imposed on φ_{pau} by stomatal closure, caused by high atmospheric vapour pressure deficit (D), soil drought and the soil nutritional state. Soil drought is defined by the ratio of water in the root zone to the maximum possible amount of water (θ). There is also a mean temperature modifier and a freeze modifier.

ii) The model calculates Net Primary Production (P_N) from P_G. For this, the model uses the proportion $P_N/P_G = \subset_{pp}$, which has been estimated as 0.47 ± 0.04 SD. This value has been shown to be relatively constant for different forest types and geographic locations (Waring *et al.* 1998).

iii) 3-PG uses simple relationships derived from the literature about root growth, fine root turnover and the effects of growing conditions on them. For this, two basic relationships have been considered: i) the inverse relationship between stem growth and the P_N fraction allocated to soil (Beets and Whitehead 1996), and ii) the effect of drought conditions and the nutritional regime on the annual allocation of carbon to root biomass, which varies from 25% to 60% (Santantonio 1989; Beets and Whitehead 1996).

iv) 3-PG uses a submodel derived from the self-thinning rule and stem growth rates to estimate changes in stand density with time (–3/2 power law, see Drew and Flewelling 1977).

v) The allocation of carbon to foliage, stem and branches is determined from the derivatives of the allometric relationship:

$$W_i = a_i W^{Ni} ,$$

where W is total biomass of the tree and i is the component of the tree (see Landsberg and Waring 1977; Sands 2000).

vi) To account for decreasing biomass productivity with age, the model invokes the negative relationship between hydraulic conductivity and P_N (Mencucini and Grace 1996). This relationship supports the hypothesis that stem conductance declines with age, inducing a lower stomatal conductance (g_c).

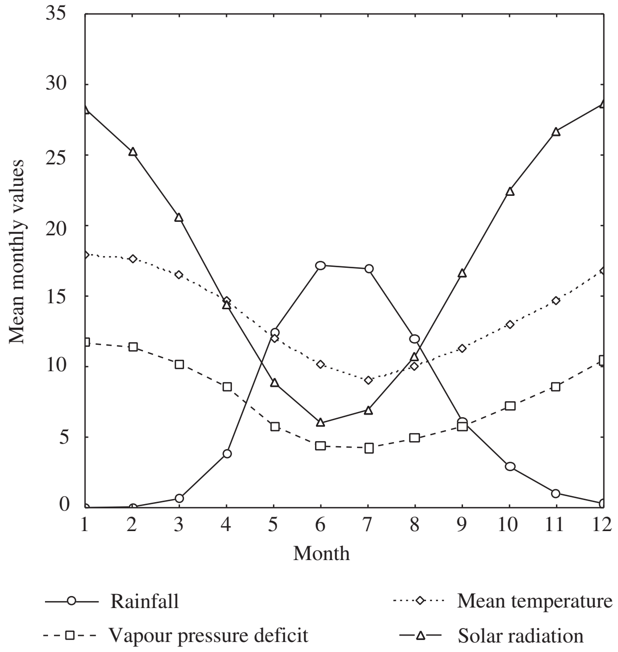


Figure 2. Total monthly precipitation (cm), mean daytime atmospheric vapour pressure deficit (mb), mean monthly temperature (ºC) and total daily solar radiation (MJ m^{-2} day^{-1}) for the Tanumé site, for the period 1983–1999

Site information for the application of the 3-PG Model

The maximum, minimum and monthly median temperatures between 1983 and 1999 were obtained from the meteorological station located next to the study area in Tanumé. The monthly mean daytime vapour pressure deficit (D) was estimated as the difference in saturated vapour pressure using the maximum and minimum monthly temperature, according to the formula given by Running *et al.* (1987):

$$\text{Saturated vapour pressure} = 0.61078 \times \exp(17.269T/(T + 273.3))\ \text{kPa}. \quad (1)$$

Estimates of monthly mean solar radiation were derived from the maximum and minimum temperature data at Tanumé, using the procedure described by Bristow and Campbell (1984). Maximum potential solar radiation on a flat surface at the study area was obtained by correcting from latitude and elevation (Running and Gower 1991). This potential value was corrected by the monthly variation of the angle of solar declination over the earth's surface (Waring 2000). Clouds and fog in the study area, which is near to the ocean, reduce the potential solar radiation. A value of 0.15 was assumed for the ratio between diffuse and direct radiation, which is considered constant during the year. The monthly values of the main meteorological variables for the study site are presented in Figure 2.

The model assumes that extraterrestrial solar radiation is double φ_{pa} and the fraction of radiation absorbed by the crown is a function of leaf area index (L), calculated from Beer's law (Landsberg and Waring 1997). The response of stomatal conductance (g_c) to environmental humidity is estimated from D (Table 2). The algorithms describing the effects of temperature and fertilisation regime on photosynthesis were modified from the original version by Sands (2000). The original authors of the model assumed that, for a given day, if temperature falls below 0ºC, there is no photosynthesis (Landsberg and Waring 1997). Sands re-wrote this constraint as:

$$f_F(d_f) = 1 - k_F(d_f/30)\ , \quad (2)$$

where the function $f_F(d_f)$ is the frost days modifier, d_f is the number of frost days in a month and, k_F is the number of days lost to photosynthetic production for every day of frost, that could be greater or less than 1.

The effect of soil fertility on photosynthesis was originally modelled by Landsberg and Waring (1997) in terms of the fraction of P_N allocated to roots: namely, as the ratio $\varphi_{pau}/\varphi_{pa}$ tends to 1, with optimum fertility and no other factors limiting, the proportion of NPP allocated to roots tends to the minimum.

This relationship was later modified to incorporate the effect of soil fertility on the efficiency with which forest canopies convert radiation to biomass, i.e. there is a direct effect of fertility on the canopy quantum efficiency (or higher utilization efficiency). Soil fertility is expressed as an index (FR) that takes values between zero (very poor fertility) and 1 (no nutrient constraints). The soil nutrition modifier is

$$f_N(\mathrm{FR}) = f_{N0} + (1 - f_{N0})\mathrm{FR}\ , \quad (3)$$

where f_{N0} is the value of f_N when FR = 0 (Sands 2000).

Sands (2000) reformulated some of the relationships of 3-PG, without changing the outcomes. He defined the effects of modifiers (ϕ) that represent age, the effects of vapour pressure deficit (f_D) and soil fertility (f_{SW}), by

$$\phi = f_{edad} \min(f_D, f_{SW})\ . \quad (4)$$

Sands (2000) expressed the effects of all environmental factors on canopy quantum efficiency by the relationship

$$\alpha_C = f_T f_F f_N \phi \alpha_C\ . \quad (5)$$

Gross Primary Production (P_G) is then determined by:

$$P_G = \alpha_C \varphi_{pau} = f_T f_F f_N \alpha\phi\varphi_{pa}\ . \quad (6)$$

Sands (2000) also introduced modifications to the formulation of litterfall and carbon allocation to root and stemwood biomass. The functional forms and parameters used in this paper are given in Table 2. The available water in the soil was estimated using water retention curves for the soil profile. Self-thinning laws are part of the model, but did not affect stand densities in this study; in the simulations we ran we used the stem populations maintained in the field.

Estimates of growth by stem analysis

Sampling

Field work was carried out from the beginning of December 1999 to April 2000. Diameter at breast height (dbh) was measured in all trees in the experimental plots. Nine trees per treatment, 36 trees in total, were randomly selected for harvesting. The dbh of each individual was measured before felling. After felling, total height (including stump height) and live crown height were measured. Disks 2–3 cm thick were cut at stump height (0.30 m),

Table 2. Model functions and parameters used in this study that may differ from the original version of 3-PG (Landsberg and Waring 1997), according to Sands (2000) for radiata pine 16 y old

Variable	Functions and parameter values	References
Fraction of radiation absorbed by canopy	$1 - (1.38 \exp(-0.5\,L))$	Landsberg and Waring (1997)
Canopy quantum efficiency	$\alpha_C = 0.055\, f_T f_F f_N \phi\, \varphi_{pa}$	Sands (2000)
Stomatal response to humidity	$g_c = g_{cmax}\,(-2.5\,D)$	Landsberg and Waring (1997)
Stomatal response to D	$fD = \exp(-0.05\,D)$	Sands (2000)
Ratio of foliage to stem	$\eta_s = 0.095\,\text{dbh} \exp((\ln 0.15/1)/\ln 10)$	Sands (2000)
Fraction of production allocated to roots (η_r)	$\eta_r = (0.8 \times 0.23)/(0.23 + (0.8 - 0.23))\, m\varphi_{pau}$	Sands (2000)
Fraction of production allocated to stem (p_{FS})	$p_{FS} = 2.4\,\text{dbh} \exp(-\log(0.15/1)/(\ln 10))$	Sands (2000)
Maximum litterfall rate (γ)	$\gamma = (0.02 \times 0.00125)/(1+\exp(-0.25t))$	Sands (2000)
Ratio NPP/GPP	0.47	Waring *et al.* (1998)
Specific leaf area	4.0 $m^2\ kg^{-1}$	Raison *et al.* (1990)
Basic density	400 $kg\ m^{-3}$	This study

L, Leaf area index, $m^2\ m^{-2}$; φ_{pa}, photosynthetically active solar radiation, MJ $m^{-2}\ mo^{-1}$; φ_{pau} photosynthetically active solar radiation utilised, MJ $m^{-2}\ mo^{-1}$; g_{cmax}, maximum stomatal conductance, m s^{-1}; g_c, stomatal conductance, m s^{-1}; D, monthly mean daily vapour deficit, kPa; m, soil fertility rank (m is 1 for fertilised soil, decreasing to 0.1 in unfertilised soils); $f_T\ f_F\ f_N\ \phi$, environmental modifiers.

Table 3. Values for precision and bias, 3-PG model validation in 16-y-old radiata pine

Treatment	Precision (REMC)		Bias (DIFA)	
	Absolute value	Percentage	Absolute value	Percentage
T1	14.4	10.9	9.7	7.3
T2	3.5	2.7	1.5	1.1
T3	3.3	4.4	0.8	0.5
T4	5.5	2.9	0.7	0.4

REMC is the square root of the quadratic mean error; DIFA is the aggregated difference; in measurement units and as a percentage

at breast height, at every 3.5 m, and at the base of the live crown. The disks were labelled and sealed in plastic bags, and stored at 2°C for later analysis.

Stem analysis

In the laboratory, the discs were saturated with water. Each was placed on an aluminium platform on which a digital camera was mounted, and photographed. Measurements were made on the digital photographs, georeferenced with geographic information system (GIS) software. The images were divided into four quadrants, allowing independent measurement of ring radii in the GIS software. The measurements were corrected for the effects of disk thickness. These measurement provided diameters at different stem heights for the annual growth periods between 1990 and 1999. Total volume for each growth period was calculated according to the geometric form of each stem section, taking stump volume as a cylinder, the breast height section as a neiloid, between breast height and the second third of the crown as a paraboloid, and the third section as a cone (Husch *et al.* 1982). To determine wood density, the disks were submerged in water to obtain fresh volume, dried at 100ºC for 48 h or until constant weight was reached, and then weighed. For estimating the stand volume, a ratio model employing basal area was used (van Laar and Akça 1997) with stem population, dbh and basal area measured annually in 44 permanent plots (11 plots per treatment) between 1990 and 1999.

The accuracy of validation of the 3-PG model was evaluated by the root mean square error (REMC) in measurement units and percentages. To evaluate bias, the Aggregated Difference (DIFA), in measurement units and percentages, was used.

Results

Validation of the model predicting volume growth

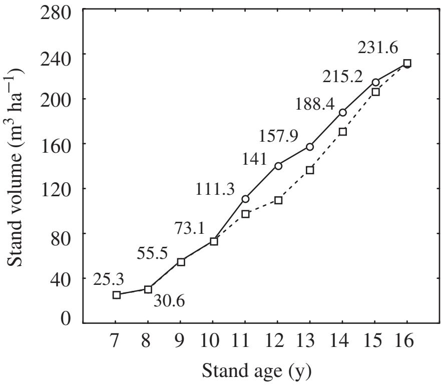
The first step of the simulation was to evaluate the model's capacity to predict volume growth. The volume growth curves estimated by stem analysis and simulated by the 3-PG model for all treatments are presented in Figure 3.

Model estimates were best in Treatments 2, 3 and 4 (T2, T3 and T4) (see Table 1). In Treatment 1 (T1) the simulation was less accurate but reached an acceptable level of precision for use in this study (<11% in REMC and <7% in DIFA). Similarly, the estimates for T2, T3 and T4 were less biased (Table 3).

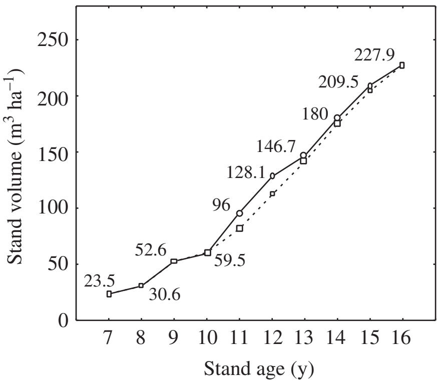
Effect of the management regime and thinning on leaf area index development and productivity

The results obtained by simulation of the development of L in the different treatments are shown in Figure 4a. The development in T4 shows the typical pattern following thinning in plantations: an increase from low values before thinning until reaching a

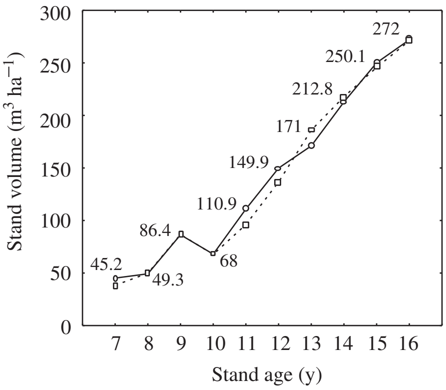
(a) Treatment 1



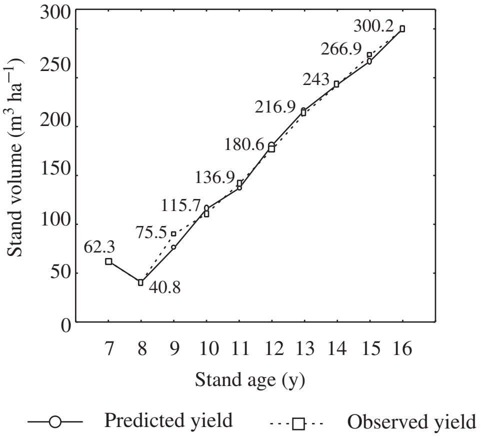
(b) Treatment 2



(c) Treatment 3



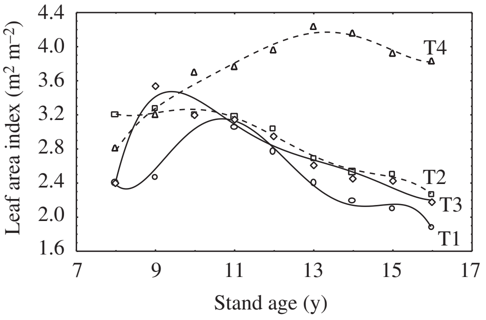
(d) Treatment 4



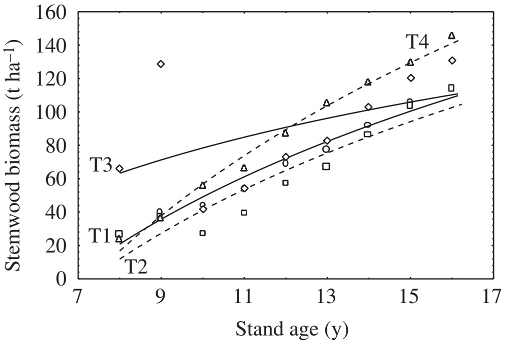
Note: Only simulated values for volumes are indicated (the correlations between estimated simulated values were: T1, $r^2 = 0.975$; T2, $r^2 = 0.992$; T3, $r^2 = 0.994$; T4, $r^2 = 0.997$)

Figure 3. Observed and simulated volume by the 3-PG model for different treatments in 16-y-old radiata pine

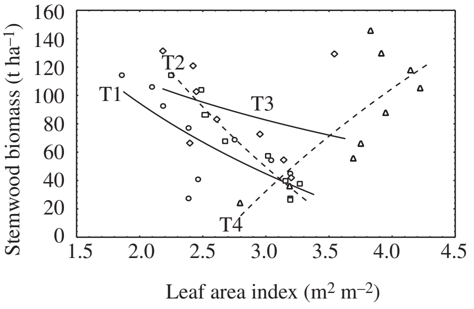
(a) Leaf area index development



(b) Stemwood biomass development



(c) Leaf area index:stemwood biomass ratio



(c) Transpiration:leaf area index ratio

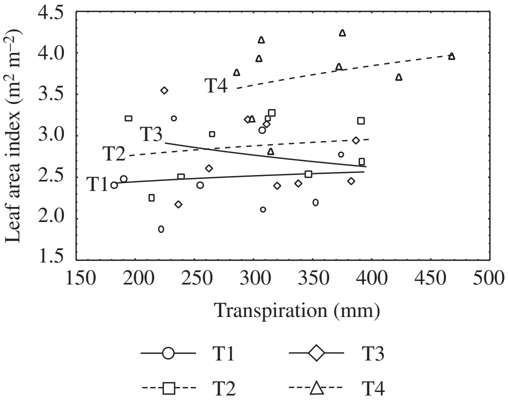


Figure 4. The effects of thinning on a) leaf area index, b) stem biomass, c) relationship of leaf area index and stem biomass, and d) relation between transpiration and leaf area index in 16-y-old radiata pine

Table 4. Simulated and observed values for diameter and mean annual volume increment, and simulated values for maximum leaf area index and the fraction of rainfall transpired in 16-y-old radiata pine

Variable	Treatment			
	T1	T2	T3	T4
Predicted dbh (cm)	38.5	39.1	41.1	28.6
Observed dbh (cm)	41.7	42.7	43.4	29.8
Predicted MAI (m^3 ha^{-1} y^{-1})	15.1	15.1	17.4	19.3
Observed MAI (m^3 ha^{-1} y^{-1})	15.1	15.1	17.5	19.3
Simulated maximum leaf area index (m^2 m^{-2})	3.3	3.2	3.5	4.2
Simulated transpiration : rainfall ratio	0.50	0.53	0.57	0.61
Soil fertility rank	1.0	0.6	1.0	0.1

Maximum available soil water capacity, 125 mm; canopy quantum efficiency, 2.3 gCMJ^{-1}, which was modified by the vapour pressure deficit, frost days and fertility ranking (in this ranking the annually fertilised stands were assigned a value of 1.0 and the unfertilised stand a value of 0.1)

plateau, and then decreasing with crown closure. In this traditionally-managed stand, L reached a maximum of 4.2 m^2 m^{-2} (Table 4) after 4 y. In the stands with silvopastoral management, the maximum L, between 3.2 and 3.5 m^2 m^{-2} (Table 4) was reached in 2 y and later decreased systematically. Annual fertilisation in T1 and T3 had positive initial effects on L (Fig. 4a) while the time course was the same in T1 and T2 where both treatments resulted in similar crown structure as a result of the similar designs of the plantation and thinning regimes (Table 1). Stem biomass systematically increased in all treatments (Fig. 4b). T4 showed the greatest increment after the last thinning, with 79.8 t ha^{-1} in a period of 5 y. The treatments in the artificial pasture silvopastoral management regime (T3 and T1) showed very similar biomass increments after thinning, with 76.7 and 76.5 t ha^{-1} respectively. However, there were no significant differences in the accumulated biomass at 16 y between the silvopastoral regimes (Fig. 4b). These results suggest that the effects of fertilisation on stem biomass were limited by crown structure. The relationship between L and stem biomass shows important differences in T4 relative to T1, T2 and T3 (Fig. 4c). In the silvopastoral stands, stem biomass decreased with increased L, but in the traditionally-managed stand stem biomass increased.

The values of the mean annual increment (MAI) observed and simulated (Table 4) are similar to those reported by Toro and Gessel (1998) for the coastal zones of granitic and metamorphic rocks for the VI Region of Chile. However, the values obtained in the different stands, 15.1 m^3 ha^{-1} y^{-1} in T1 and T2, and 19.3 m^3 ha^{-1} y^{-1} in T4, illustrated the effects of silvicultural regime and the management of site resources on productivity. The highest MAI, in the T4 treatment, is attributed to the higher residual stem population. In the silvopastoral regimes, T1 and T2, which had the same stem population but different fertilisation regimes and grassland types, MAI was the same. However, MAI was 12% higher in T3 than T1, a difference attributed to the plantation design. Likewise, T4 shows the influence of final stem population on dbh: values are around 38.5% lower than the mean dbh of the stands with silvopastoral management (Table 4).

Transpiration values in all treatments were in agreement with those reported by Teskey and Sheriff (1996) (Table 4). The similar ratios of transpiration : precipitation found in T1 and T2 at 16 y old were lower than those found in T4. In general, final stand density and leaf area index were the most important factors in determining water consumption at stand level (Fig. 4d). In semiarid zones and eroded soils on granitic and metamorphic rocks, such as this study area, water is the most important factor limiting productivity. However, modelling shows that 125 mm of available water in the soil is enough to increase stand productivity.

Discussion

Validation of the model predicting volume growth

The 3-PG model provides good predictions of stand volume, showing reliable estimates, low errors and no bias (Table 4). Because the self-thinning law determines stand density in the model, simulation of the effect of thinning on growth requires several runs, using re-set stem values, to evaluate stand properties through time. However, the 3-PG model proved a valuable tool for the analysis of radiata pine stand development because it provided data (Table 4) that traditional statistical models cannot.

Both specific leaf area and wood density are known to vary with site and climate, but the values of 4 m^{-2} kg^{-1} for specific leaf area and 400 kg m^{-3} for wood density did not influence the final results of the simulations.

Effect of the management regime and thinning on leaf area index development and productivity

The development of L was found to be significantly different between the stands under the traditional forestry management regime and the silvopastoral regimes (Fig. 4a). In this respect, it is reasonable to expect a homogenous distribution of trees in space, as in the T4 treatment, to reach the potential L and intercept maximum radiation (Grace *et al.* 1987). In stands under silvopastoral regimes the plantation design and fertilisation regime allowed the crowns to reach their maximum size. Maximum values of L were not different between silvopastoral treatments because of the similar structures of crowns and the final stand density after thinning (Table 1). These results agree with those of Vose and Allen (1988) who found that the course of development of L, and the potential L, are highly dependent on stand density, the size of the trees and the supply of site resources. In this study the crown structure and density after thinning did not allow the potential L to be reached, even though soil fertility was improved.

All the treatments increased stem biomass after thinning. However, the stand under the traditional forestry regime showed a different pattern of development of stem biomass when compared with the silvopastoral regimes (Fig. 4c). It appears that the increment of stem biomass is a function of growth efficiency and L (Mäkelä *et al.* 2000b). Furthermore, there is a direct relationship between φ_{pau} and dry matter production (Grace *et al.* 1987). Therefore, it is to be expected that thinning will have positive effects on the increment of L and growth efficiency, which explains the higher stem biomass (Waring and Running 1998). Thinning in T4 caused increased L and increased growth efficiency, but in stands under silvopastoral regimes thinning had an initial effect in the development of L only in T3, as can be seen in Figure 4a. McMurtrie and Landsberg (1992) hypothesized that fertilisation, in traditionally managed stands, increases L and stem biomass, and that L is solely limited by water and nutrients. However, our results do not support this in the stands with silvopastoral regimes, because L was constrained by crown structure (due to plantation design) and low final stand density (Table 4).

The increase in stem biomass was greater in T3 than in T1 and T2 in the silvopastoral regimes. This is because T3 was a row design which allowed greater development of crowns compared with the cluster designs of T1 and T2 (Table 1). The greater biomass found in T1 relative to T2 reflects the fact that, where there is competition for nutrients, the fertilisation regime has a positive effect, despite limitations of crown structure. The results of this study therefore suggest that, for radiata pine established on poor soils, the factors determining increases in stem biomass and MAI are canopy leaf mass, crown structure (Perry 1985; Cannel 1989), and final stand density (Vose and Allen 1988; Landsberg and Gower 1997). The data from the silvopastoral regimes suggest that fertilisation has effects on L, but the limit is determined by crown structure and stand density. The effect of fertilisation in increasing stem biomass can also be explained by a decrease in fine root biomass (Santantonio and Santantonio 1987; Beets and Whitehead 1996) and lower water consumption in the silvopastoral regimes (Waring and Schlesinger 1985; Waring 1987; Oliver and Larson 1996; Waring and Running 1998).

It is generally assumed that in semiarid zones an increment in productivity will be associated with water consumption. In this study the maximum available water in the soil was the same in all treatments, but MAI values at 16 y were higher in the traditional forestry regime than in the silvopastoral ones (Table 4). The results of the simulations showed that silvopastoral stands consumed less water than stands with traditional management. These results are consistent with those Eastham *et al.* (1990), who indicated that the balance of productivity and water use between trees and pasture is regulated by tree population density and not by tree size (Table 1; Fig. 4d). The results are also consistent with those of Teskey and Sheriff (1996), who showed that large trees extract water from the same soil volume as small trees. Furthermore, water consumption in stands of radiata pine is highly correlated with water availability in the first metre of soil. Increased water use efficiency is therefore attributed to a decrease in the rate of fine root turnover, as appears to be the case in T3 in the silvopastoral regimes.

Conclusions

The development and maximum values of leaf area index, L, were shown to be strongly controlled by plantation design and final stand density. Fertilisation had positive effects on leaf area index, as long as it was not limited by crown structure. Because of the strong relationship between photosynthetically active radiation and dry matter production (Grace *et al.* 1987), the site occupancy by crowns explains the rate of wood production in the traditionally-managed forestry stand (Vose and Allen 1988). In the fertilisation treatment, when maximum L was reached, stands temporarily increased their stem biomass at the expense of fine root biomass, even though water availability was still limiting (Santantonio and Santantonio 1987; Beets and Whitehead 1996). Final wood production was affected by thinning, which caused changes in stand development through its effect on crown structure and site resources availability. The maximization of wood production depends on the joint management of site resources, thinning intensity and timing (Snowdon and Benson 1992). Growth simulation by process-based models is a valuable tool. However, it is important to include thinning in the modelling, because the self-thinning law operates over a longer time than is of interest in plantations of fast-growing species.

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References

Beets, P.N. and Whitehead, D. (1996) Carbon partitioning in *Pinus radiata* stands in relation to leaf nitrogen status. *Tree Physiology* **6,** 131–138.

Bristow, K.L. and Campbell, G.S. (1984) On the relationship between incoming solar radiation and daily maximum and minimun temperature. *Agricultural and Forest Meteorology* **32,** 159–166.

Cannel, M.G.R. (1989) Physiological basis of wood production: a review. *Scandinavian Journal of Forest Research* **4,** 459–490.

Carlyle, C. (1995) Managing site resources to maximise the productivity of *Pinus radiata* plantations. Paper to 6th Silvotecna-Expocorma, Concepción, Chile, 27–28 November 1995.

Coops, N.C. and Waring, R.H. (2001) Estimating forest productivity in the eastern Siskiyou Mountains of southwest Oregon using a satellite driven process model, P-PGS. *Canadian Journal of Forest Research* **31,** 143–154.

Coops, N.C., Waring, R.H. and Landsberg, J.J. (1998) Assessing forest productivity in Australia and New Zealand using a physiologically-based model driven with averaged monthly weather data and satellite-derived estimates of canopy photosynthetic capacity. *Forest Ecology and Management* **104,** 113–127.

Drew, T.J. and Flewelling, J.W. (1977) Some recent Japanese theories of yield–density relationship and their applications to Monterey pine plantations. *Forest Science* **23,** 517–534.

Eastham, J., Rose, C.W., Charles-Edwards, D.A., Cameron, D.M. and Rance, S.J. (1990) Planting density effects on water use efficiency of trees and pasture in an agroforestry experiment. *New Zealand Journal of Forestry Science* **1,** 39–53.

Grace, J., Jarvis, P.G. and Norman, J.M. (1987) Modelling the interception of solar radiant energy in intensively managed stands. *New Zealand Journal of Forestry Science* **17,** 193–209.

Husch, B., Miller, C. and Beers, T. (1982) *Forest Mensuration*. Krieger Publishing. New York, USA. 402 pp.

Landsberg, J.J. and Hingston, F.J. (1996) Evaluating a simple radiation/dry matter conversion model using data from *Eucalyptus globulus* plantations in Western Australia. *Tree Physiology* **16,** 801–808.

Landsberg, J.J. and Gower, S.T. (1997) *Applications of Physiological Ecology to Forest Management.* Academic Press, San Diego, USA. 354 pp.

Landsberg, J.J. and Waring, R.H. (1997) A generalised model of forest productivity using concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management* **95,** 209–228.

Landsberg, J.J., Johnson, K.H., Albaugh, T.J., Allen, H.L. and McKeand, S.E. (2000) Applying 3-PG, a simple process-based model designed to produce practical results, to data from loblolly pine experiments. *Forest Science* **47,** 43–51.

Mencuccini, M. and Grace, J. (1996) Hydraulic conductance, light interception and needle nutrient concentration in a Scots pine stand and their relations with net primary productivity. *Tree Physiology* **16**, 459–468.

Mäkelä, A., Landsberg, J.J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Ägren, G.I., Oliver, C.D. and Puttonen, P. (2000a) Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. *Tree Physiology* **20,** 289–298.

Mäkelä, A., Sievänen, R., Lindner, M. and Lasch, P. (2000b) Application of volume growth and survival graphs in the evaluation of four process-based models. *Tree Physiology* **20,** 347–355.

McMurtrie, R.E., Rook D.A. and Kelliher, F.M. (1990) Modelling the yield of *Pinus radiata* on a site limited by water and nitrogen. *Forest Ecology and Management* **30,** 381–413.

McMurtrie, R.E. and Landsberg, J.J. (1992) Using a simulation model to evaluate the effects of water and nutrients on the growth and carbon partitioning of *Pinus radiata. Forest Ecology and Management* **52,** 243–260.

Oliver, C.D. and Larson, B.C. (1996) *Forest Stand Dynamics*. John Wiley and Sons, New York. 520 pp.

Perry, D.A. (1985) The competition process in forest stands. In: Cannel, M.G.R. and Jackson, J.E. (eds). *Attributes of Trees as Crop Plants*. Institute of Terrestrial Ecology, Penicuick, pp. 481–506.

Raison, R.J., Khanna, P.K., Connell, M.J. and Faulkiner, R.A. (1992). Effects of water availability and fertilization on nitrogen cycling in a stand of *Pinus radiata. Forest Ecology and Management* **30,** 31–43.

Roberts, S.D., Long, J.N. and Smith, F.W. (1993) Canopy stratification and leaf area efficiency: a conceptualization. *Forest Ecology and Management* **60,** 143–156.

Running, S.W. and Gower, S.T. (1991) Forest-BGC, a general model of forest ecosystem process for regional applications II. Dynamic carbon allocations and nitrogen budgets. *Tree Physiology* **9,** 147–160.

Running, S.W., Nemani, R.R. and Hungerford, R.D. (1987) Extrapolation of synoptic meteorological data in mountain terrain and its use for simulating forest evapotranspiration and photosynthesis. *Canadian Journal of Forest Research* **17,** 472–483.

Sands, P.J. and Landsberg, J.J. (2001) Parameterisation of 3-PG for plantation grown *Eucalyptus globulus. Forest Ecology and Management* **163,** 273–292.

Sands, P. (2000) *3PGpjs — a user-friendly interface to 3-PG, the Landsberg and Waring model of forest productivity.* Cooperative Research Centre for Sustainable Production Forestry and CSIRO Forestry and Forest Products. Technical Report 29. Tasmania, Australia. 16 pp.

Santantonio, D. (1989) Dry-matter partitioning and fine-root production in forests — new approaches to a difficult problem. In: Pereira, J.S. and Waring, R.H. (eds). *Biomass Production by Fast-Growing Trees.* Kluwer Academic, Dordrecht, pp. 57–72.

Santantonio, D. and Santantonio, E. (1987) Seasonal changes and dead fine roots during two successive years in a thinned plantation of *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science* **17,** 315–328.

Snowdon, P. and Benson, M.L. (1992) Effects of combinations of irrigation and fertilisation on the growth and above-ground biomass production of *Pinus radiata*. *Forest Ecology and Management* **52,** 87–116.

Teskey, R.O. and Sheriff, D.W. (1996) Water use by *Pinus radiata* trees in a plantation. *Tree Physiology* **19,** 273–279.

Toro, J. and Gessel, S. (1998) Radiata pine plantations in Chile. *New Forests* **18,** 33–44.

van Laar, A. and Akça, A. (1997) *Forest Mensuration*. Cuvillier Verlag, Göttingen. 418 pp.

Vose, J.M. and Allen, H.L. (1988) Leaf area, stemwood growth, and nutrition relationships in loblolly pine. *Forest Science* **34,** 547–563.

Wang, Y.P. and Jarvis, P.G. (1990) Influence of crown properties on PAR absorption, photosynthesis and transpiration in sitka spruce: Application of a model (MAESTRO). *Tree Physiology* **7,** 297–316.

Waring, R.H. (1987) Characteristics of trees predisposed to die. *BioScience* **37,** 569–574.

Waring, R.H. (2000) A process model analysis of environmental limitations on the growth of sitka spruce plantations in Great Britain. *Forestry* **73,** 65–79.

Waring, R.H. and Running, S.W. (1998) *Forest Ecosystems: Analysis at Multiple Scales*. Academic Press. San Diego. 370 pp.

Waring, R.H. and Ryan, M.G. (1995) Carbon balance modeling. *Encyclopedia of Energy and the Environment* **4,** 480–491.

Waring, R.H. and Schlesinger, W.H. (1985) *Forest Ecosystems*. Academic Press, New York. 339 pp.

Waring, R.H., Landsberg, J.J. and Williams, M. (1998) Net primary production of forest: a constant fraction of gross primary production? *Tree Physiology* **18,** 129–134.

White, J.D., Coops, N.C. and Scott, N.A. (2000) Estimates of New Zealand forest and scrub biomass from the 3-PG model. *Ecological Modeling* **131,** 175–190.